



First records of *Tropidurus madeiramamore* Carvalho, Paredero, Villalobos-Chaves, Ferreira, Rodrigues & Curcio, 2024 (Squamata, Tropiduridae) from Bolivia

Robert P. Langstroth¹, Mauricio Herrera², Gabriel Callapa³, Luis R. Rivas⁴, Lucindo Gonzales², Lesly López⁵, Anthony R. DiMeglio⁶, Gregory Schneider⁶, Robert B. Wallace⁷

¹ Independent researcher, South Riding, Virginia, United States of America

² Museo de Historia Natural Noel Kempff Mercado, Universidad Autónoma Gabriel René Moreno, Santa Cruz de Sierra, Bolivia

³ Bolivian Amphibian Initiative, Cochabamba, Bolivia

⁴ Centro de Investigación de Recursos Acuáticos, Universidad Autónoma del Beni José Ballivián, Trinidad, Beni, Bolivia

⁵ Colección Boliviana de Fauna, Museo Nacional de Historia Natural, Universidad Mayor de San Andrés, La Paz, Bolivia

⁶ Museum of Zoology, University of Michigan, Ann Arbor, Michigan, United States of America

⁷ Wildlife Conservation Society, Bolivia Program, La Paz, Bolivia

Corresponding author: Robert P. Langstroth (pampa_isla@yahoo.de)

Abstract. This note reports the first country records of *Tropidurus madeiramamore* Carvalho, Paredero, Villalobos-Chaves, Ferreira, Rodrigues & Curcio, 2024 for Bolivia, all northern Beni Department, extending the range by some 300 km to the west of earlier records, clarifying the status of specimens previously reported in the literature as *Tropidurus oreadicus* Rodrigues, 1987, and providing comments on the biogeographic and conservation values of the Amazonian savannas of the Beni.

Key words. Amazonia, Beni, biogeography, Cerrado, lizards, savannas

Langstroth RP, Herrera M, Callapa G, Rivas LR, Gonzales L, López L, DiMeglio AR, Schneider G, Wallace RB (2025) First records of *Tropidurus madeiramamore* Carvalho, Paredero, Villalobos-Chaves, Ferreira, Rodrigues & Curcio, 2024 (Squamata, Tropiduridae) from Bolivia. Check List 21 (2): 467–474. <https://doi.org/10.15560/21.2.467>

INTRODUCTION

Tropidurus Wied-Neuwied, 1824 is a widespread genus of lizards in South American savannas and dry forests east of the Andes (Carvalho 2013). As of late 2024, *Tropidurus* comprised 31 recognized species in four species groups based on molecular phylogenetic estimates (Carvalho et al. 2024). The *Tropidurus torquatus* group is a monophyletic clade comprising 18 species, of which only three were recognized before 1982: *T. torquatus* (Wied-Neuwied, 1820), *T. hispidus* (Spix, 1825), and *T. hygomi* Reinhardt and Lütken, 1861 (Carvalho et al. 2024). Rodrigues (1987) described seven new species in the *T. torquatus* group, including *T. oreadicus* Rodrigues, 1987, which was conceived as a widespread species of the Brazilian Cerrado, ranging as far west as the Madeira River at Porto Velho. However, Rodrigues (1987) cautioned that the populations from Porto Velho and other open formation enclaves of Amazonia south of the Amazon River should be only provisionally attributed to *T. oreadicus*.

Harvey and Gutberlet (1998) described three new species of *Tropidurus* from the lowlands of Bolivia (*T. callathelys* Harvey and Gutberlet, 1998, *T. chromatops* Harvey and Gutberlet, 1998, *T. xanthochilus* Harvey and Gutberlet, 1998) and provided a key to the species of the genus recognized at the time. Their characterization of *T. oreadicus* was based on four specimens from a series of six housed at the University of Michigan Museum of Zoology (UMMZ) and Harvey and Gutberlet did not provide locality data for the specimens examined. We note that Harvey and Gutberlet (2000) described and illustrated a unique scale surface microstructure in the UMMZ series. While neither Harvey and Gutberlet (1998) nor Dirksen and De la Riva (1999) had included *T. oreadicus* as a species present in Bolivia, Langstroth (2005) included it as a probable species for Bolivia based on an unseen specimen in the Colección Boliviana de Fauna catalogued as *T. oreadicus* from the Beni Department. Subsequent to the publication of Langstroth (2005), we discovered that the *T. oreadicus* specimens examined by Harvey and Gutberlet (1998) were in fact catalogued with the locality of "Ribaulti, Bolivia" and we also examined a specimen diagnosable as *T. oreadicus* collected from the Beni Department of Bolivia in October 2005 and deposited in the Museo Noel Kempff Mercado. Eversole et al. (2024) included



Academic editor: Rafael de Fraga
Received: 9 January 2025
Accepted: 21 March 2025
Published: 24 April 2025

Copyright © The authors. This is an open-access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International – CC BY 4.0)

T. oreadicus in their specimen-based list of the reptiles of the Beni Department but indicated that the record is questionable.

Carvalho et al. (2024) revisited the taxonomy of the populations from Rondônia that had been tentatively assigned to *T. oreadicus* by Rodrigues (1987) and found them to be genetically and morphologically distinct from the *T. oreadicus* of the central Cerrado and described them as *T. madeiramamore*, which they characterized as a highly polymorphic species endemic to savanna enclaves of Rondônia. In addition, Carvalho et al. (2024: 34) stated that “*Tropidurus* populations morphologically similar to *T. madeiramamore* have never been reported to the Bolivian Amazonia” citing Dirksen and De la Riva (1999) and other works; however, they did not mention the University of Michigan Museum of Zoology specimens included as *T. oreadicus* by Harvey and Gutberlet (1998), the specimen from the Beni Department that Langstroth (2005) included as a probable Bolivian record of *T. oreadicus*, or the specimen at Museo Noel Kempff Mercado.

Given the description of *T. madeiramamore*, we find it necessary to reexamine the identity of the Bolivian material mentioned above and additional specimens collected more recently. In this note, we compare these specimens against the description of *T. madeiramamore*, provide novel information on their localities and habitats, and comment on the significance of our findings.

METHODS

We examined specimens of *Tropidurus* collected in 1922, 1995, 2005, and 2023 in the Beni Department, Bolivia, and housed in the University of Michigan Museum of Zoology (UMMZ), Colección Boliviana de Fauna del Museo Nacional de Historia Natural (CBF), and Museo de Historia Natural Noel Kempff Mercado (MNKR). All specimens were determined initially using the keys of Rodrigues (1987) and Harvey and Gutberlet (1998) and found to correspond to *T. oreadicus* and then compared against the description of *T. madeiramamore* (Carvalho et al. 2024). In addition, the senior author visited the city of Guajará-Mirim, Rondônia, in February 2024, and opportunistically photographed a free-living *T. madeiramamore* (not captured) reported herein. The specimens examined were confirmed by the *Tropidurus* specialist Andre LG Carvalho. In addition, we prepared the distribution map of *Tropidurus madeiramamore* with QGIS v. 3.16.3 (QGIS 2025).

RESULTS

***Tropidurus madeiramamore* Carvalho, Paredero, Villalobos-Chaves, Ferreira, Rodrigues & Curcio, 2024**

Figures 1, 2, 4A

New records. BOLIVIA — BENI • Ballivián Province, Santa Rosa Municipality, Estancia Villa Camba; 13°10'11"S, 066°38'31"W; 160 m alt.; 12.X.1995; W. Hanagarth & C. Rosales leg.; 1♀, CBF 1764 • Ballivián Province, Santa Rosa Municipality, 15.9 km NW of Puerto Teresa; 13°23'01"S, 066°43'59"W; 167 m alt.; X.2005; M. Herrera leg.; in laterite crust savanna; 1♀, MNKR 3758 • Ballivián Province, Santa Rosa Municipality, 1.7 km N of Buena Hora; 13°03'35.57"S, 66°30'27.59"W; 165 m alt.; 20.IX.2023; G. Callapa obs.; 10 adult individuals observed on termite mounds in savanna • Ballivián Province, Santa Rosa Municipality, Villa Fátima; 12°58'45.74"S, 066°30'59.24"W; 166 m alt.; 19.IX.2023; G. Callapa & F. Guarayo leg.; 1♂, CBF 4646 • Vaca Diez Province, Riberalta Municipality, unspecified locality (cataloged as “Ribualti”); 1922; 2♂, 2♀, 2 juveniles, UMMZ 57699 • Yacuma Province, Exaltación Municipality, 800 m E of Villa Fátima; 12°58'47.06"S, 066°30'37.52"W; 167 m alt.; 21.IX.2023; G. Callapa & F. Guarayo leg.; 1♂, CBF 4647; on termite mound in savanna with heavy cattle grazing.

Additional record. BRAZIL — RONDÔNIA • Guajará-Mirim Municipality, Guajará-Mirim, Highway BR-425, 140 m northeast of the intersection of Avenida 38; 10°45'23.68"S, 065°18'27.75"W; 141 m alt.; 27.II.2024. R. Langstroth obs.; on a concrete curb of driveway to an electrical substation; juvenile, photographs.

UMMZ 57699 specimens (Figure 1A–D) is a series of six specimens recorded in the ledger as *Tropidurus torquatus* with the locality of “Ribualti, Bolivia”, without a collector, collection date, or accession number. While the following two numbers in the ledger, UMMZ 57700 (*Iguana iguana* (Linnaeus, 1758)) and UMMZ 57701 (*Thecadactylus solimoensis* Bergmann & Russel, 2007), are also from “Ribualti, Bolivia”, the ledger indicates that UMMZ 57699–700 were received from the “Williamson Expedition” (in both cases indicated by ditto signs) and that UMMZ 57701 was collected by the “Mulford Expedition” (indicated in writing). In his June 1922 Report of the Director to the Board of Regents, Ruthven (1922) noted that the Museum had contributed to two expeditions that yielded important zoological material: the University of Michigan-Williamson Expedition to western Brazil and the Mulford Biological Exploration of the Amazon Basin. Both expeditions, essentially simultaneously in early 1922, visited the upper Madeira Basin in what is presently the state of Rondônia, Brazil, and the Beni Department of Bolivia.

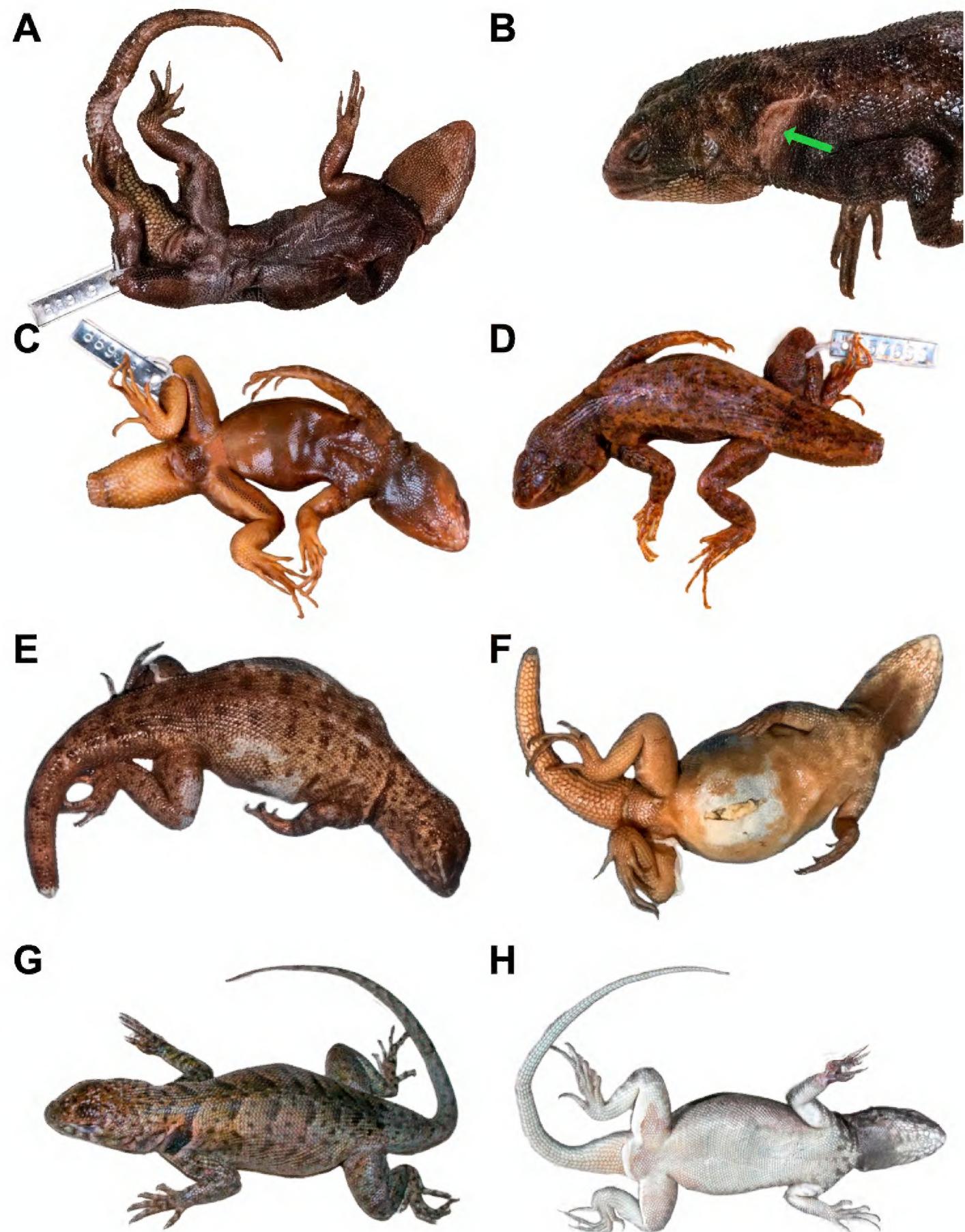


Figure 1. *Tropidurus madeiramamore*. **A.** UMMZ 57699-a, venter, snout-vent length (SVL) = 101 mm. **B.** UMMZ 57699-a, arrow indicates the single deep oblique neck fold pocket. **C.** UMMZ 57699-c, venter, SVL = 89 mm. **D.** UMMZ 57699-c, dorsum. **E.** CBF 1764, dorsum. **F.** CBF 1764, venter, SVL = 65 mm. **G.** MNKR 3758, dorsum. **H.** MNKR 3758, venter, SVL = 72 mm.

"Ribaulti" is most certainly a misspelling of "Riberalta", a city on the Beni River at the confluence with the Madre de Dios in the Beni Department, some 80 km WSW of the city of Guajará-Mirim, Rondônia. The Mulford Exploration was based in Riberalta for much of January and February of 1922 (Snyder 1926) and then downriver at Cachuela Esperanza the first two weeks of March of 1922 before returning to New York via the Madeira and Amazon rivers (White 1922). Ichthyologist Nathan E. Pearson and entomologist William M. Mann were members of the Mulford Exploration (White 1922). UMMZ holds many herpetological specimens collected by Pearson and a smaller number by Mann. For example, UMMZ 57704 is an *Anolis meridionalis* Boettger, 1885 collected by Pearson in October 1921 from the savannas near Reyes in the Beni Department (Langstroth 2006) and UMMZ 57705 is an *Oxyrhopus petolarius* (Linnaeus, 1758) collected by Mann in the tropical Andes of La Paz during an earlier leg of the expedition. Most of Pearson's material are fish and amphibians from the Ixon River, which discharges into the Beni River just upstream of Riberalta.

While the Mulford team was busy along the Beni River in Bolivia, Jesse H. Williamson, leader of the University of Michigan–Williamson Expedition to western Brazil, collected an impressive series of *Tropidurus* (UMMZ 56802, 56804–07, 56817, 56836–41) downstream at Porto Velho, Rondônia, on various dates between 24 January and 10 May 1922. Frost (1992) included UMMZ 56805 in his sample of *T. oreadicus* for his phylogenetic assessment of the Tropiduridae. While Williamson did collect dragonflies at Cachuela Esperanza ("Rio Beni, Cashuela Esperanza") and a *Ceratophrys cornuta* (Linnaeus, 1758) at nearby Villa Bella in April 1922, we find no evidence that he collected any *Tropidurus* specimens from Bolivia.

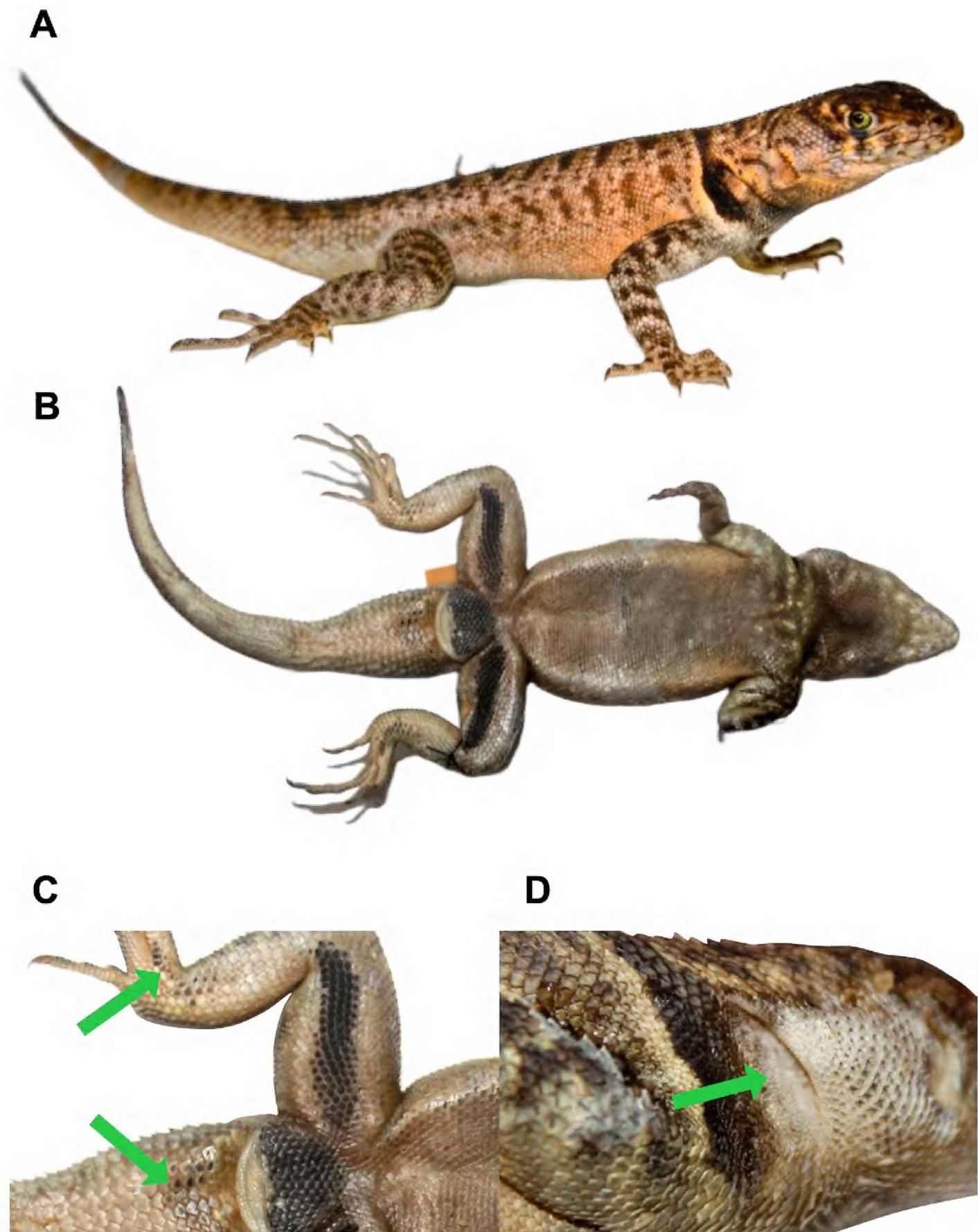


Figure 2. *Tropidurus madeiramamore*, Villa Fátima, Beni, Bolivia. **A.** In life (CBF 4646, SVL = 76 mm). **B.** Venter (CBF 4647, SVL = 93 mm). **C.** Detail of flash marks, arrows indicating characteristic black pigmentation on base of tail and first toe (CBF 4647). **D.** Single deep oblique neck fold pocket (CBF 4647).

Based on the available information, we consider it most probable that the UMMZ 57699 series was obtained by the Mulford Exploration from the vicinity of Riberalta, Bolivia, between January and March of 1922.

CBF 1764 specimen (Figure 1E, F) was reported by Langstroth (2005) as probable evidence for the presence of *T. oreadicus* in Bolivia, but he was unable to examine the specimen. While the locality reported by the CBF catalog in 2005 was "Yacuma Province, Northern Beni", it was later changed to "Vaca Diez Province, El Pico Nuevo, near the Río Benicito". However, "El Pico Nuevo" is a rubber and Brazil nut camp deep in the interior of an extensive forest area some 21 km W of the Benicito (Defense Mapping Agency 1989), a locality that is not likely to support open-formation *Tropidurus*. Also, we are unaware of any evidence that the collectors ever visited or collected in the forests near El Pico Nuevo. Rather, the available information indicates that on 13 October 1995, the day after CBF 1764 was collected, Hanagarth and Rosales collected plants at Estancia Villa Camba (Figure 5), a cattle ranch in an upland savanna with microrelief dominated by termite and worm mounds, 39 km N of the Río Yata and 4 km towards the Río Benicito, east of the highway to Riberalta (Tropicos.org. Missouri Botanical Garden 2024). Based on the available, information, we conclude that CBF 1764 was collected in the vicinity of Estancia Villa Camba in the savannas of the upper Río Benicito drainage.

MNKR 3758 specimen (Figure 1G, H) was collected in 2005 during surveys for Blue-Throated Macaws (*Ara glaucogularis* Dabbene, 1921) in an extensive savanna about 7 km N of the Yata River and 8.7 km W of highway F8, some 25–26 km WSW of the locality we approximate for CBF 1764 (Figure 5). Beyond the laterite outcrop where the lizard was found, there are extensive seasonally inundated *Mauritia flexuosa* L.f. palm savannas in poorly drained bottomlands. The rock-like laterite crust has an appearance reminiscent of a lava flow

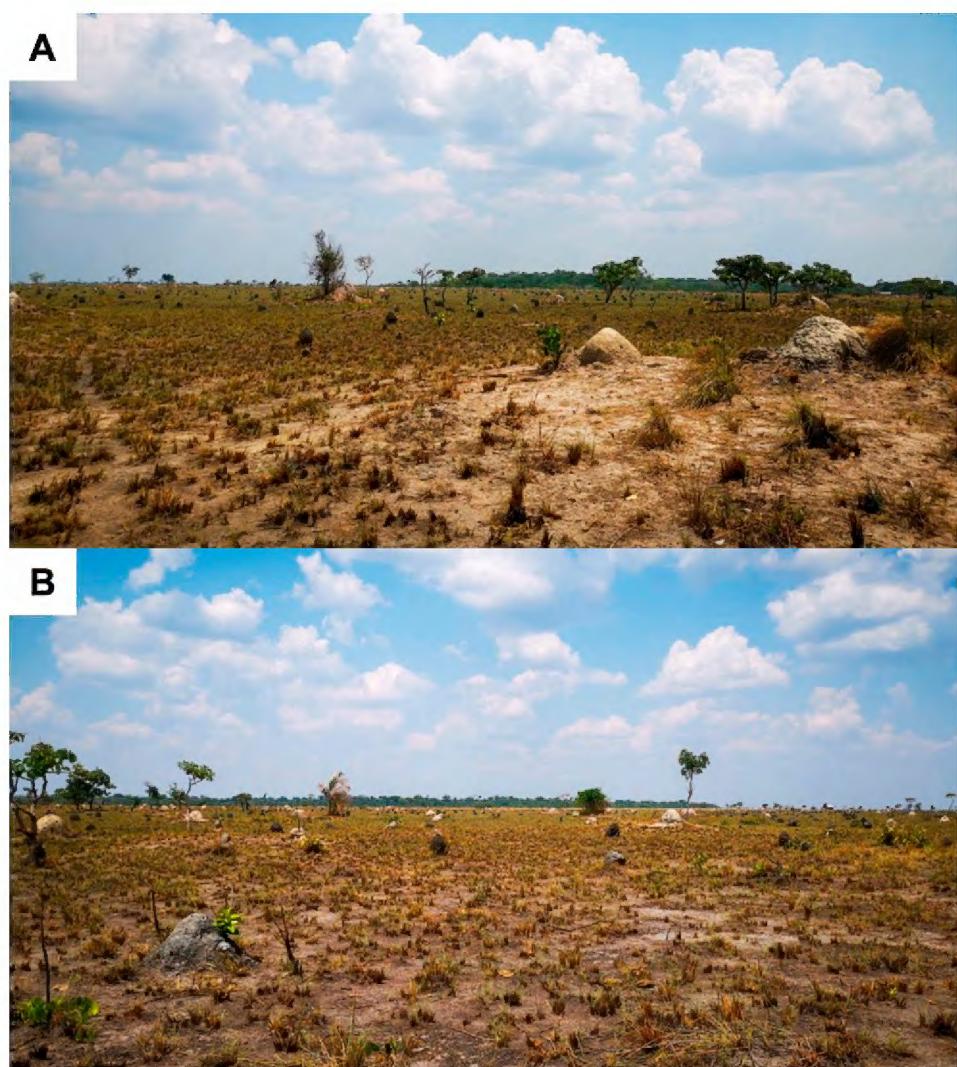


Figure 3. Habitats of *Tropidurus madeiramamore* at Villa Fátima, Beni, Bolivia, 19 September 2023.



Figure 4. *Tropidurus madeiramamore*, Guajará-Mirim, Rondônia, Brazil, 27 February 2024. **A.** Specimen in life (not collected). **B.** Urbanized habitat along highway BR-425 where the specimen was photographed.

and was largely devoid of vegetation except for scattered grasses in cracks. The lizard was found upon the exposed crust near the edge of the outcropping near some trees to which it fled upon pursuit.

CBF 4646–47 specimens (Figure 2) were collected in 2023 during surveys of the savannas of the upper Biata, Benicito, and Yata river drainages organized by the Wildlife Conservation Society (WCS) and the Grupo de Trabajo para los Llanos de Moxos. The specimens were captured on termite mounds in a heavily grazed and burned savanna approximately 1.5 km E of the Benicito at the Villa Fátima ranch (Figures 3A, B, 5). Ten additional *Tropidurus madeiramamore* were observed in a similar habitat 1.7 km N of Buena Hora, some 10 km to the SSW of Villa Fátima, approximately 1.0 km W of the Benicito River, and 15.2 km NE of the CBF 1764 locality (Figure 5). Upon disturbance, nearly all the lizards took refuge in tunnels in the termite mounds from which they could not be extricated. One individual, however, fled its mound and climbed the trunk of a ca. 3 m tree to about 1.5 m above ground. Most lizards were observed in the late afternoon, but a few were found in the morning hours. Many of the lizards were observed moving their heads up and down while posing facing the sun.

Guajará-Mirim. In February 2024, we visited the city of Guajará-Mirim, Rondônia, and photographed a juvenile *Tropidurus madeiramamore* found basking in the morning sun on the curb of the driveway of an electrical substation, some 25 m from the edge of the BR-425 highway (Figure 4A, B). The site is on the alluvial terrace of the Mamoré River and was a formerly forested habitat, not a rock outcrop or savanna enclave. The nearest known *T. madeiramamore* localities reported by Carvalho et al. (2024) are on outcrops of the Serra dos Parecis, some 5.2–6.2 km ENE of the urban substation reported here.

Identification. The specimens reported above from the northern part of the Beni Department (UMMZ 57699, CBF 1764, MNKR 3758, and CBF 4646–47) were all unequivocally determined as *T. oreadicus* using the keys of Rodrigues (1987) and Harvey and Gutberlet (1998). This latter outcome was inevitable given that Harvey and Gutberlet developed their key using four specimens from the UMMZ 57699 series as the sole exemplars of *T. oreadicus*. We examined the specimens in further detail and found them all to correspond to *T. madeiramamore* based on the complete agreement of external morphological and coloration characters described by Carvalho et al. (2024), as well as the historical biogeographic continuity observed between the northern Beni savannas and the Amazonian savanna enclaves of Rondônia (Langstroth 2011; Werneck et al. 2012). The Bolivian specimens reported here all possess a single deep oblique neck fold mite pocket and lack axillary or inguinal folds or pockets, a character combination that distinguishes them from all species of the *T. torquatus* group except for *T. madeiramamore* and *T. oreadicus*. Figures 1B, 2D illustrate the nature of this pocket in specimens from the vicinity of Riberalta and the Benicito-Yata basin, respectively. The specimens reported here can be distinguished from *T. oreadicus* by (i) a wider and deeper later neck mite pocket, (ii) a

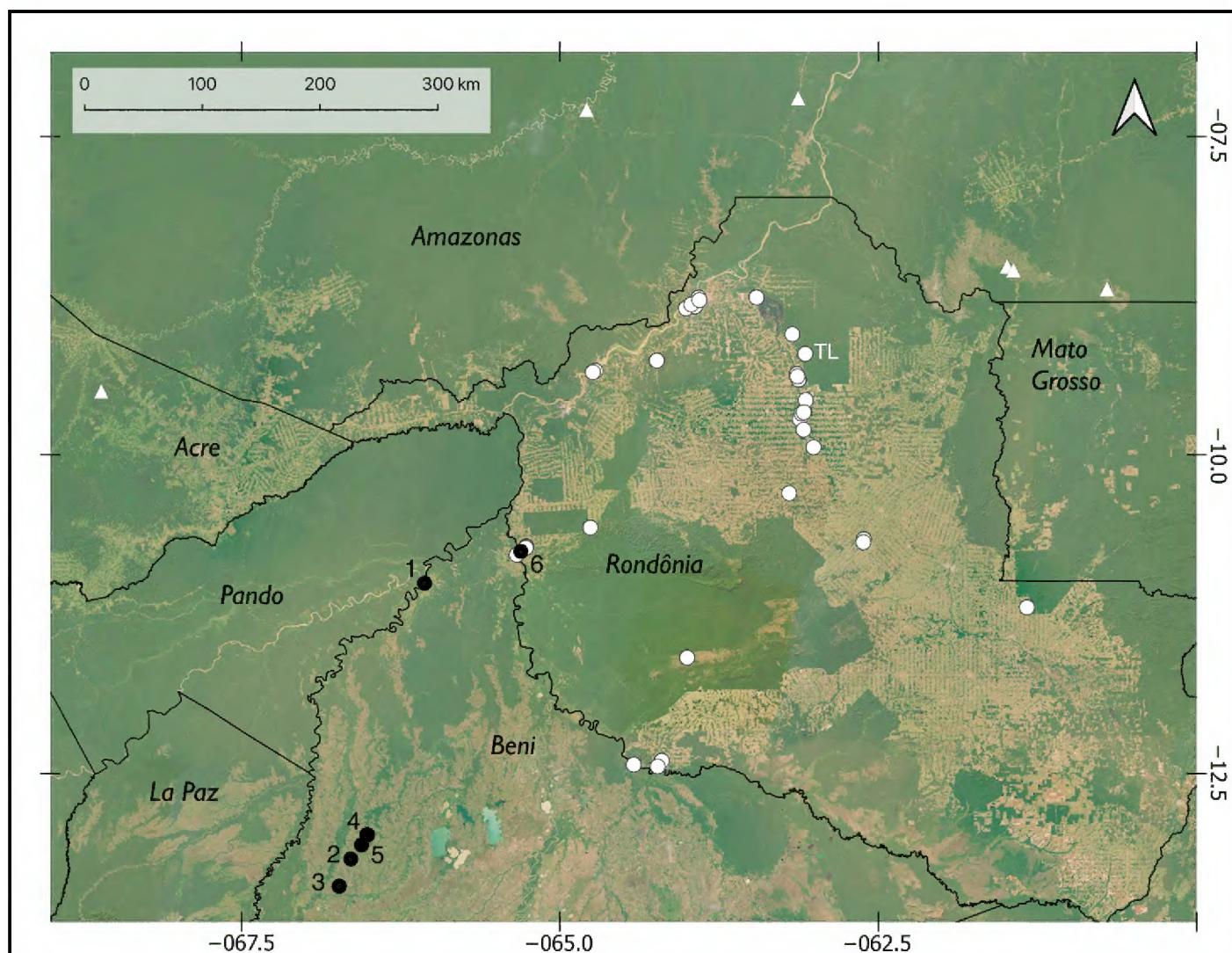


Figure 5. Reported localities of *Tropidurus madeiramamore*. White circles = verified localities reported by Carvalho et al. (2024); TL = type locality; white triangles = unverified localities reported by Carvalho et al. (2024); black circles = new records: 1 = Riberalta (approximate provenance of the UMMZ 57699 series); 2 = Estancia Villa Camba (CBF 1764); 3 = laterite savanna 7 km N of Yata River (MKNR 3758); 4 = Villa Fátima (CBF 4646–47), 5 = Buena Hora (GC observations); 6 = Guajará-Mirim (Figure 4). Markers may indicate multiple localities. Black lines indicate subnational administrative units (states of Acre, Amazonas, Mato Grosso, and Rondônia, Brazil; departments of Beni, La Paz, and Pando, Bolivia).

tendency towards ventral melanism (especially more extensive dark pigmentation in the gular region versus a more localized medial dark spot in *T. oreadicus*), and (iii) the presence, in four adult males (SVL = 76–101 mm), of black pigmentation on the ventral face of the tail near the cloaca (Figure 2C), and, in one adult male (SVL = 93 mm), black pigmentation at the base of the first toe (Figure 2C), all of which are character states consistent with *T. madeiramamore* (Carvalho et al. 2024). The adult females (SVL = 65–96 mm) display light venters with dark grey pigmentation in the gular region and chest, similar to the V1 and V2 patterns of Carvalho et al. (2024). Despite its discoloration due to preservation for over a century, a juvenile (SVL = 33 mm) of the UMMZ series displays the white lateroventral band (F1) observed in some *T. madeiramamore* but unknown in *T. oreadicus* (Carvalho et al. 2024).

DISCUSSION

The previous specimen-based records for *Tropidurus madeiramamore* are summarized by Carvalho et al. (2024) who considered the species to be endemic to the State of Rondônia, Brazil, with the possible exception of a few unverified records in the Brazilian states of Amazonas and Acre (Figure 5). Our new records demonstrate that *T. madeiramamore* is neither endemic to Rondônia nor to Brazil and extend its known distribution into the savannas of the Beni Department of Bolivia, some 290 km WSW of the closest Brazilian locality along Iténez/Guaporé River (Forte Príncipe da Beira/Costa Marques) and 330 km SW of Guajará-Mirim on the Mamoré. Furthermore, Carvalho et al. (2024) reported urban populations only from the vicinity of the city of Porto Velho and from Itapuã do Oeste and we report here an urban population from the city of Guajará-Mirim, Rondônia, along the Mamoré River and the Bolivian border. As reported by de Andrade (2019), urbanized environments can present important opportunities for some species of *Tropidurus*, which appears to be the case for at least some populations of *T. madeiramamore*.

In addition to *T. madeiramamore*, the northern Beni savannas support populations of *Anolis meridionalis* (Langstroth 2006) and *Kentropyx vanzoi* Gallagher & Dixon, 1980 (Langstroth 2011), species considered to be endemic to the Cerrado (Nogueira et al. 2011) and found in some savanna enclaves of Rondônia (Gainsbury and Colli 2003). The presence of a “Cerrado Arc” extending from Rondônia westward into the Beni and La Paz departments of Bolivia is evidenced by these lizards as well as the soils, vegetation, birds, and mammals (Hanagarth 1993; Hanagarth and Beck 1996; Langstroth Plotkin 2011; Bezerra and Pardiñas 2016). Werneck et al. (2012) considered the Beni Savannas to be an area of climatic stability that served as a Cerrado refugium. The presence of *A. meridionalis*, *K. vanzoi*, and *T. madeiramamore* in both the extensive Beni Savannas and the relictual savanna enclaves of Rondônia suggests that the Beni Savannas have served as a stable refugium for elements of the savanna biota whose habitats in Rondônia have decreased in extent, connectivity, and diversity as the result of both natural and anthropogenic causes (Gainsbury and Colli 2003). Clearly, the

Beni Savannas are a globally important large-scale reservoir of the biodiversity of the “little known, highly threatened and under-protected” Amazonian savannas (de Carvalho and Mustin 2017).

Finally, our findings demonstrate the continued relevance of historical and ongoing biological collections to biodiversity science. Much of the world remains poorly sampled and biodiversity data remain woefully incomplete. At the same time, collections made over a century ago still contain hidden gems such as the lizards collected by the Mulford Biological Exploration of the Amazon and the University of Michigan–Williamson Expedition to western Brazil. It is critical to continue to bridge the gaps between legacy collections (and researchers) and current and future generations of biodiversity scientists, especially in the countries with remote areas rich in under-studied biodiversity.

ACKNOWLEDGEMENTS

We dedicate this paper to the memory of Werner Hanagarth (1948–2003), a pioneer in the biogeography and ecology of the Beni Savannas and mentor to a generation of Bolivian scientists and conservationists. We thank the curatorial staff at UMMZ, CBF, and MNK for their assistance with photographing specimens and searching through catalog and field notes. We particularly thank André Luiz Carvalho for his feedback, discussions, and insights. We thank the Wildlife Conservation Society and the Gordon and Betty Moore Foundation for funding the scientific expedition to the Biata, Yata, and Benicito rivers. Finally, we thank the anonymous reviewers of the manuscript.

ADDITIONAL INFORMATION

Conflict of interest

The authors declare that no competing interests exist.

Ethical statement

No ethical statement is reported.

Funding

The fieldwork of G. Callapa was financially supported by the Wildlife Conservation Society.

Author contributions

Conceptualization: RPL. Formal analysis: LRR, RPL. Investigation: GC, LRR, LL, LG, MH, RPL, TD. Methodology: RPL. Resources: GC, GS, LL, MH, RBW. Visualization: GC, LL, LRR, RPL, TD. Writing – original draft: RPL. Writing – review and editing: GC, LRR, LL, LG, MH, TD, RBW.

Author ORCID iDs

Robert P. Langstroth  <https://orcid.org/0000-0003-3935-2495>

Gabriel Callapa  <https://orcid.org/0009-0004-9361-3216>

Luis R. Rivas  <https://orcid.org/0000-0002-3156-9705>

Lucindo Gonzales  <https://orcid.org/0000-0001-6329-2889>

Robert B. Wallace  <https://orcid.org/0000-0001-7411-6338>

Data availability

All data that support the findings of this study are available in the main text.

REFERENCES

Bezerra AMR, Pardiñas UFJ (2016) *Kunzia tomentosus* (Rodentia: Cricetidae). Mammalian Species 48(930): 1–9. <https://doi.org/10.1093/mspecies/sev013>

Carvalho ALG (2013) On the distribution and conservation of the South American lizard genus *Tropidurus* Wied-Neuwied, 1825 (Squamata: Tropiduridae). Zootaxa 3640 (1): 42–56. <https://doi.org/10.11646/zootaxa.3640.1.3>

Carvalho ALG, Paredero RCB, Villalobos-Chaves D, Ferreira E, Rodrigues, Curcio FF (2024) A highly polymorphic South American collared lizard (Tropiduridae: *Tropidurus*) reveals that open–dry refugia from south-western Amazonia staged allopatric speciation. Zoological Journal of the Linnean Society 201: 493–533. <https://doi.org/10.1093/zoolinnean/zlad138>

de Andrade AC (2019) Metropolitan lizards? Urbanization gradient and the density of lagartixas (*Tropidurus hispidus*) in a tropical city. Ecology and Evolution 10: 1740–1750.

de Carvalho WD, Mustin K (2017) The highly threatened and little known Amazonian savannahs. Nature Ecology & Evolution 1: 0100. <https://doi.org/10.1038/s41559-017-0100>

Defense Mapping Agency (1989) Estancia Firmeza, Bolivia [map], Edition 1-DMA, 1:100,000, Series H632, Sheet 3747. Defense Mapping Agency, Washington, DC. https://maps.lib.utexas.edu/maps/topo/bolivia/estancia_firmeza-bolivia-100k-1989.pdf. Accessed on: 2025-01-29.

Dirksen L, De la Riva I (1999) Los saurios y anfibios de Bolivia (Reptilia, Squamata): lista patrón, localidades y bibliografía. Graellsia 55: 199–215.

Eversole CB, Powell RL, Rivas LR, Lizarro DE (2024) Reptile biodiversity and vulnerability in Bolivia's Beni Department: informing conservation priorities in a neglected frontier. *Diversity* 16: 335. <https://doi.org/10.3390/d16060335>

Frost DR (1992) Phylogenetic analysis and taxonomy of the *Tropidurus* group of lizards (Iguania: Tropiduridae). *American Museum Novitates* 3033: 1–68.

Gainsbury AM, Colli GR (2003) Lizard Assemblages from natural cerrado enclaves in southwestern Amazonia: the role of stochastic extinctions and isolation. *Biotropica* 35: 503–519. <https://doi.org/10.1111/j.1744-7429.2003.tb00607.x>

Hanagarth W (1993) Acerca de la geoecología de las sabanas del Beni. Instituto de Ecología, La Paz, Bolivia, 186 pp.

Hanagarth W, Beck SG (1996) Biogeographie der Beni-Savannen (Bolivien). *Geographische Rundschau* 48: 662–668.

Harvey MB, Gutberlet, RL (1998) Lizards of the genus *Tropidurus* (Iguania: Tropiduridae) from the Serranía de Huanchaca, Bolivia: new species, natural history, and a key to the genus. *Herpetologica* 54: 493–520.

Harvey MB, Gutberlet, RL (2000) A phylogenetic analysis of the tropidurine lizards (Squamata: Tropiduridae), including new characters of squamation and epidermal microstructure. *Zoological Journal of the Linnean Society* 128: 89–233. <https://doi.org/10.1006/zjls.1999.0203>

Langstroth RP (2005) Adiciones probables y confirmadas para la saurofauna boliviana. *Kempffiana* 1: 101–128.

Langstroth RP (2006) Notas sobre *Anolis meridionalis* Boettger, 1885 (Squamata: Iguania: Polychrotidae) en Bolivia y comentarios sobre *Anolis steinbachi*. *Kempffiana* 2: 154–172.

Langstroth Plotkin R (2011) Biogeography of the Llanos de Moxos: natural and anthropogenic determinants. *Geographica Helvetica* 66: 183–192. <https://doi.org/10.5194/gh-66-183-2011>

Nogueira C, Ribeiro S, Costa GC, Colli GR (2011) Vicariance and endemism in a Neotropical savanna hotspot: distribution patterns of Cerrado squamate reptiles. *Journal of Biogeography* 38: 1907–1922. <https://doi.org/10.1111/j.1365-2699.2011.02538.x>

QGIS (2025) QGIS Geographic Information System. QGIS Association. <http://www.qgis.org>. Accessed on: 2025-01-22.

Rodrigues MT (1987) Sistemática, ecología e zoogeografía dos *Tropidurus* do grupo *torquatus* ao sul do Rio Amazonas (Sauria, Iguanidae). *Arquivos de Zoologia* 3: 105–230. <https://doi.org/10.11606/issn.2176-7793.v3i3p105-230>

Ruthven AG (1922) Report of the Director of the Museum of Zoology to the Board of Regents, July 1, 1921 to June 30, 1922. *University Bulletin, New Series* 24(14): 1–39.

Snyder TE (1926) Termites collected on the Mulford Biological Exploration to the Amazon Basin, 1921–1922. *Proceedings of the United States National Museum* 68 (2615): 1–76. <https://doi.org/10.5479/si.00963801.68-2615.1>

Tropicos.org, Missouri Botanical Garden (2024) Collection Event: W. Hanagarth (608064). <https://tropicos.org/collectionevent/608064> Accessed on: 2024-07-01.

Werneck FP, Nogueira C, Colli GR, Sites Jr JW, Costa GC (2012) Climatic stability in the Brazilian Cerrado: implications for biogeographical connections of South American savannas, species richness and conservation in a biodiversity hotspot. *Journal of Biogeography* 39: 1695–706. <https://doi.org/10.1111/j.1365-2699.2012.02715.x>

White OE (1922) Botanical exploration in Bolivia. *Brooklyn Botanic Garden Record* 11: 93–105.